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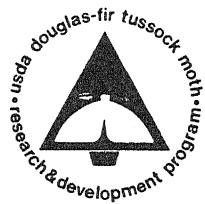
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EFFECT OF DEFOLIATION BY THE DOUGLAS-FIR TUSSOCK MOTH ON MOISTURE STRESS IN GRAND FIR AND SUBSEQUENT ATTACK BY THE FIR ENGRAVER BEETLE (COLEOPTERA: SCOLYTIDAE)^{1/}

by

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Abstract

The moisture status of grand fir trees defoliated artificially and by the Douglas-fir tussock moth was measured using the pressure bomb technique. Measurements were made from the time of defoliation through the 2 following years. The daily maximum moisture stress was significantly reduced by defoliation in the year of defoliation, but was not significantly affected in the following 2 years. Daily minimum plant moisture stress was not altered significantly. Other variables significantly correlated with moisture stress were vapor pressure deficit, crown class, tree height, and needle length.

Fir engraver attacks and survival in defoliated trees were not correlated with high moisture stress.

KEYWORDS: Plant-moisture relations, defoliation damage, Douglas-fir tussock moth, *Orygia pseudotsugata*, fir engraver beetle, *Scolytus ventralis*, grand fir, *Abies grandis*.

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INTRODUCTION

Insect defoliation of forest trees can result in growth loss, defect, and mortality of defoliated trees (Wickman 1958 and 1963, Wickman and Scharpf 1972). Much of the mortality may be due to bark beetles which attack the weakened trees (Wickman 1958, 1963) and may subsequently develop into epidemics causing further losses (Patterson 1929, Berryman 1973, Dewey et al. 1974). Most species of bark beetles require trees to be under physiological stress before they can make successful attacks (Caird 1955, Rudinsky 1962, Kozlowski 1969, Berryman 1972). In California, Wickman (1958) studied the mortality of white fir, *Abies concolor* (Gordon and Glendenon Lindley), defoliated by the Douglas-fir tussock moth (*Orgyia pseudotsugata* McDunnough) and found that 75 percent of all trees that died were infested by the fir engraver beetle (*Scolytus ventralis* LeConte) and flatheaded and roundheaded borers. In addition, Berryman (1973) concluded that tussock moth outbreaks were a major cause of fir engraver epidemics in grand fir, *Abies grandis* (Douglas) Lindley, in northern Idaho.

Stand and environmental factors, including insect defoliation, have been found to influence plant moisture stress (PMS) of trees (Stephens et al. 1972; Wambolt 1973). High PMS has been correlated with successful bark beetle attack (Vite 1961, Stoszek 1973, Ferrell 1974).

Redmond (1959) found that spruce budworm defoliation resulted in mortality of balsam fir rootlets. Conceivably, this could result in water stress during refoliation in the years following defoliation due to root-crown imbalance. The objective of the present study was to test the hypotheses that moisture stress increases in direct relationship to percent defoliation in the years during and following outbreaks of the Douglas-fir tussock moth and that bark beetle attacks are associated with this increased moisture stress.

MATERIALS AND METHODS

Experimental Plots

Four plots defoliated by the tussock moth were chosen to represent different intensities and years of defoliation. Mensurational data for these plots are given in table 1. In addition to this information the following variables were measured on each sample tree: crown class, crown ratio, 1974 basal area growth, and needle lengths in 1975. Percent defoliation was visually estimated. Vapor pressure deficit was also recorded on the plots at the time of sampling.

Table 1--Summary of measurements made on each plot

Plot	Mean plot mensurational data				Date	PMS measurements				Years since last defoliation
	D.b.h. (inches)	Height (feet)	Age (years)	Percent grand fir		Time ^{1/}	1	2	3	
North-South	10.2	47.3	82	--	0-45	IX-3-74	--	--	X	7
Palouse Divide	8.4	50.2	50	45.7	0-45	VIII-20-74	X	X	X	5
Twin Buttes	10.6	68.1	61	62.2	2/ ¹⁰⁻⁸⁰	VIII-23-74 VIII-22-75	X	X	X	6
Fox Prairie	4.7	29.1	55	78.1	3/ ⁰⁻⁹⁵	VIII-10-75 VIII-8-75	X	--	X	5
Artificial defoliation	5/	6.1	5/	5/	0-100	VII-25-75 IX-5-75	--	--	X	12
						IX-5-75	X	--	X	12
										0

^{1/}1 = presunrise, 2 = midmorning, 3 = midafternoon, 4 = sunset. An X indicates measurements were made.

^{2/}This plot was defoliated with approximately equal intensity in 72 and 73.

^{3/}Suffered two years of defoliation but only final (73) defoliation known.

^{4/}One additional tree measured in midafternoon only.

^{5/}Not measured because only simple regressions done with data from this plot.

The North-South plot, located on the St. Joe National Forest in northern Idaho, was used to determine the immediate effects of defoliation. The Palouse Divide plot located near the North-South plot, and the Twin Buttes plot on the Umatilla National Forest in southeastern Washington, were used to measure moisture status of trees in the year following the last defoliation. None of these plots were defoliated heavily enough to cause significant tree mortality and fir engraver beetle populations were rather low. In order to correlate beetle attack with PMS, the Fox Prairie plot on the Umatilla National Forest in northeastern Oregon was added in 1975. Many grand fir on this plot had been attacked by the fir engraver beetle in 1974.

A plot of artificially defoliated trees was set up near Harvard, Idaho to measure the physiological effects of defoliation by carefully controlled experiments. Twelve trees were defoliated by clipping the foliage with scissors on July 17 and 18, 1975. The trees were sparsely distributed, open grown, and all vegetation was removed around each one to minimize variation due to competition. Defoliation intensities were 99, 67, 33, and 0 percent of the total crown area with three replicates per defoliation class. The foliage was removed from the top down which is similar to the pattern of tussock moth defoliation. Artificial defoliation, however, does not necessarily mimic natural tussock moth defoliation.

Plant Moisture Stress

The pressure bomb method was used to evaluate moisture stress of defoliated trees (Scholander et al. 1965, Waring and Cleary 1967). This procedure measures the negative pressure on the column of water in the xylem. Plant moisture stress is defined as the absolute value of the negative xylem pressure.

Naturally defoliated trees were selected as close together as possible but had suffered different amounts of defoliation. Three twigs were removed from each tree using a pole pruner or a 12-gauge shotgun; one from the top third of the crown, one from the middle third, and one from the lower third. PMS was measured immediately following twig removal. Only twigs with needles were used, although many of the twigs had received some defoliation. Daylight readings were taken from sunlit portions of the crown. The readings from each tree were averaged to give one value per tree. A single midcrown branch was used to measure PMS on the artificially defoliated trees.

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the exception that the North-South
end of defoliation, and the Fox
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flight in 1975. (See table 1 for dates and the times measurements were taken.)

Fir Engraver Beetle Attacks

Each tree on the Fox Prairie plot was carefully examined on July 9-10, August 14, and October 1, 1975, for external evidence of bark beetle attack. The plots were visited again in the summer of 1976, and the dead trees were felled and sampled using the techniques of Berryman (1973).

Statistical Analysis

Linear regression and correlation were used to determine the effects of each independent variable on PMS. Trial calculations and graphical analysis indicated all relationships were approximately linear within the ranges measured. Multiple regression and correlation were used to determine the combined effects of the independent variables on moisture stress. Differences in PMS means between crown levels were analyzed using the t test.

RESULTS

Grand fir exhibited a daily PMS cycle of increasing stress from sunrise until midafternoon followed by a decrease until sunrise, a pattern which has been observed in many plants (Scholander et al. 1965, Klepper 1968, Lassoie 1973, Hellkvist et al. 1974). The daily grand fir PMS was highly correlated with vapor pressure deficit of the air ($r=0.827$, $p<0.001$, $N=20$, $Y=5.17+0.60X$).

The Year of Defoliation

Maximum daytime moisture stress during the season of defoliation was significantly decreased by both tussock moth and artificial defoliation (fig. 1). Artificial defoliation did not reduce PMS until it exceeded 33 percent. Minimum PMS, which occurs in the early morning, was not significantly affected by defoliation ($r=0.138$, $p>0.10$).

Multiple regression analysis of the North-South data revealed that defoliation was the most important variable in determining maximum PMS, explaining 72.6 percent of the variation (table 2).

The maximum (afternoon) PMS of naturally defoliated crown tops was significantly lower than that of the undefoliated bases ($\bar{X}(\text{top})=12.2$ atm., $\bar{X}(\text{base})=15.1$ atm., $t=6.7$, $p<0.01$). In undefoliated trees, however, this

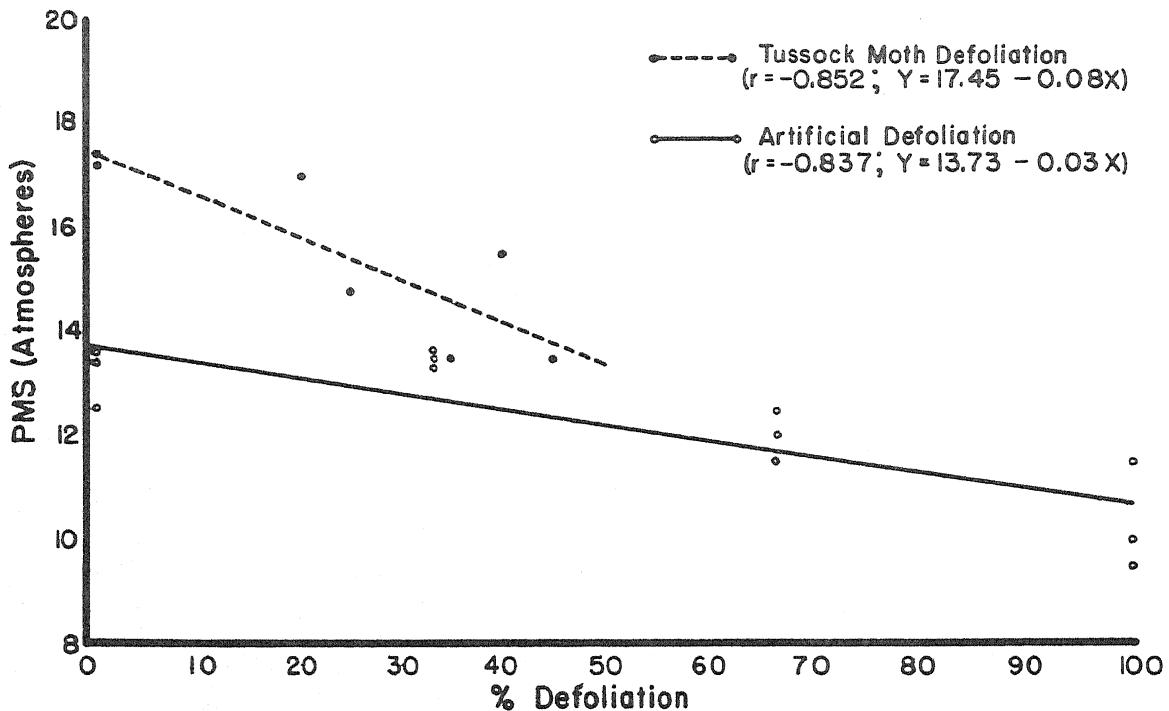


Figure 1.--The effect of current defoliation on daily maximum plant moisture stress; correlation coefficients significant at the 0.05- (tussock moth defoliation) and 0.01- (artificial defoliation) levels.

relationship was reversed (\bar{X} (top)=19.0 atm., \bar{X} (base)=15.8 atm., $t=19.0$, $p<0.01$).

The afternoon PMS of artificially defoliated trees was not altered until defoliation surpassed 33 percent (fig. 1). This is because only one midcrown branch was measured and the defoliation did not extend down to midcrown until the trees were defoliated more than 33 percent. The relationship between artificial defoliation and PMS was remarkably similar on the two sampling dates; i.e., July 25, $r=-0.837$, $Y=13.73 - 0.03X$, $\bar{X}=12.25$ (fig. 1) September 5, $r=-0.648$, $P<0.05$, $Y=14.3 - 0.02X$, $\bar{X}=13.29$.

One Year Following Defoliation

The influence of defoliation on PMS was considerably reduced in the year after defoliation. Neither early morning nor midafternoon PMS was significantly affected by percentage defoliation (tables 2 and 3). However, there was a tendency for morning (minimum) PMS to be directly associated with defoliation suggesting that increased stress may occur in the year following defoliation.

Table 2--Simple and multiple correlation between selected independent variables and mid-afternoon (daily maximum) plant moisture stress from the year of defoliation through the 2 following years

Years since last defoliation	Statistic	Variable and order of entry into multiple regression model 1/							
		1	2	3	4	5	6	7	8
0	Simple r	-0.552**	-0.619	0.507	-0.609	0.004	-0.167	-0.140	7
	Percent variation explained by model (100R ²)								
1	Simple r	0.737***	0.001	0.412	0.112	-0.004	0.419	-0.354	-0.191
	Percent variation explained by model (100R ²)								
2	Simple r	0.354	-0.338	-0.030	0.193	0.084	0.053	0.046	0.061
	Percent variation explained by model (100R ²)								

1/Variables were added in decreasing order of importance to regression model according to their contribution to R².

2/No plot variable because only the North-South plot was used for this year's data.

3/Zero degrees of freedom.

*, **, *** Significant at the 0.1-, 0.5-, and 0.01-levels, respectively.

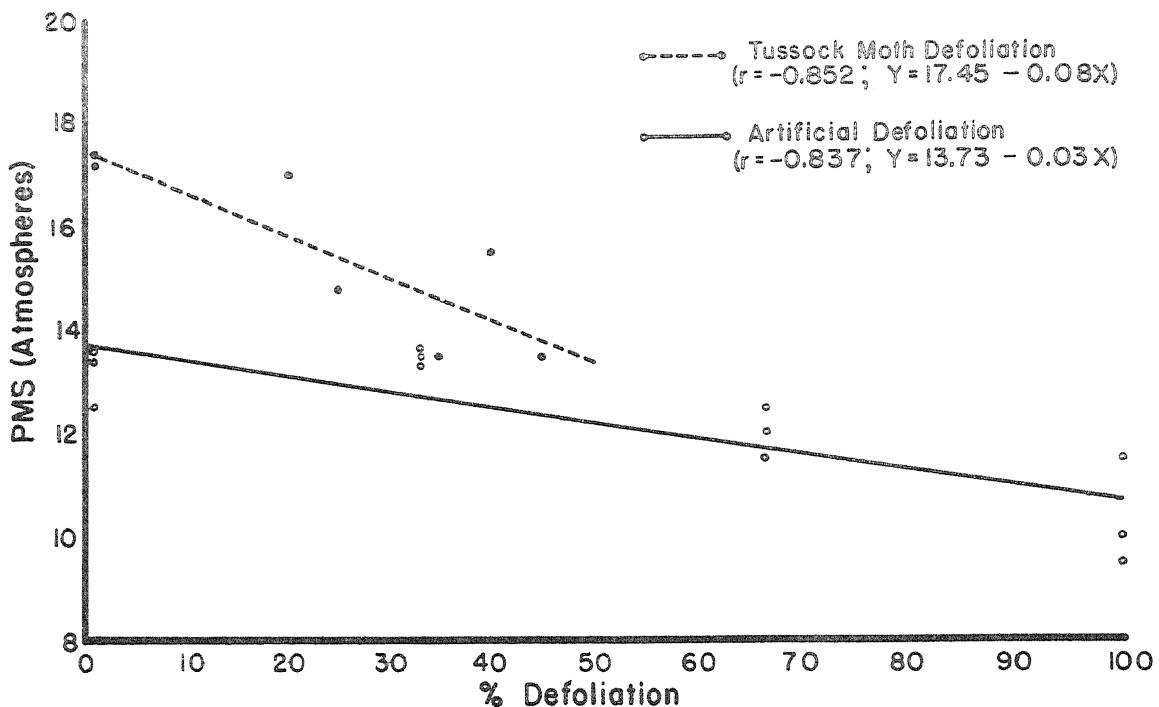


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		Variable and order of entry into multiple regression model ^{1/}								
Years since last defoliation	Statistic	1	2	3	4	5	6	7	8	N
0	Defoliation									
	Simple r	-0.352**	-0.619	0.507	-0.609	0.004	-0.167	-0.140		7
Percent variation explained by model (100R ²)	Percent variation explained by model (100R ²)	72.6**	94.6***	98.5***	99.5**	3/	3/	3/		
	Crown class									
1	Age									
	Simple r	0.737***	0.001	0.412	0.112	-0.004	0.419	-0.354	-0.191	11
Percent variation explained by model (100R ²)	Percent variation explained by model (100R ²)	54.3***	71.0***	89.6***	93.2***	93.5***	94.1***	96.3**	96.4	
	Growth rate									
2	Plot									
	Simple r	0.354	-0.338	-0.030	0.193	0.084	0.053	0.046	0.061	19
Percent variation explained by model (100R ²)	Needle length									
	Crown class									
3	Height									
	Defoliation									

^{1/}Variables were added in decreasing order of importance to regression model according to their contribution to R².

^{2/}No plot variable because only the North-South plot was used for this year's data.

^{3/}Zero degrees of freedom.

*, **, *** Significant at the 0.1-, 0.5-, and 0.01-levels, respectively.

Table 3--Simple and multiple correlation between selected independent variables and predawn (daily minimum) plant moisture stress for 1 and 2 years following defoliation

Years since last defoliation	Statistic	Variable and order of entry into multiple regression model ^{1/}								
		1	2	3	4	5	6	7	8	N
	D.b.h.									
1	Simple r	0.734***	0.629**	0.393	0.155	0.555*	0.197	0.081	-0.082	11
Percent variation explained by model (100R ²)		53.9***	69.9***	82.7***	84.7***	85.7***	86.6**	86.7*	87.4	
	Crown class									
	Defoliation									
	Age									
	Height									
	Plot									
	Crown ratio									
	Growth rate									
	Needle length									
	Plot									
	Crown class									
2	Simple r	-0.513**	0.248	0.336	0.012	-0.052	0.080	-0.073	-0.103	20
Percent variation explained by model (100R ²)		26.3**	31.0**	35.5**	38.0**	38.8**	41.9**	44.6**	46.9**	

^{1/}Variables were added in decreasing order of importance to regression model according to their contribution to R².

*, **, *** Significant at the 0.1-, 0.05-, and 0.01-levels, respectively.

In addition, percent defoliation was the third most important variable in determining early morning PMS (table 3). On the other hand, afternoon (maximum) PMS still exhibited a tendency towards an inverse relationship to defoliation (table 2).

Two Years Following Defoliation

The correlation between percent defoliation and afternoon (maximum) PMS in the 2d year following defoliation was insignificant (table 2). Although not statistically significant, there was a tendency for more heavily defoliated trees to have higher early morning (minimum) PMS measurements (table 3). The only significant correlation was between needle length and early morning PMS which indicated that trees with shorter needles had higher stress levels (table 3). There was also a strong negative interaction between percent defoliation and needle length ($r=-0.982$, $P<0.001$) on the Fox Prairie plot, suggesting that defoliation may have a more significant effect on early morning PMS than the analysis indicates.

Bark Beetle Attacks

All but one of the sample trees on the Fox Prairie plot received at least one *S. ventralis* attack by October 1, 1975, and of these, three died (table 4). Only heavily defoliated trees were successfully attacked, but there appeared to be no correlation between PMS and tree mortality, beetle attacks, or beetle survival.

Table 4--Plant moisture stress and *S. ventralis* attacks and survival in Douglas-fir tussock moth defoliated *A. grandis*

Tree	PMS				Attack success	Beetle data from killed trees			
	9-10 July 75		14 August 75			Attacks/ ft ²	Emergence ft ²	Emergence attacks x 2	
	AM	PM	AM	PM					
C1	4.2	12.2	6.3	15.7	unsuccessful	--	--	--	
C2	4.8	11.3	4.8	16.8	unsuccessful	--	--	--	
C3	3.8	10.3	4.5	17.0	unsuccessful	--	--	--	
1	5.7	16.2	4.2	16.8	not attacked	--	--	--	
2	6.5	17.5	6.0	17.3	unsuccessful	--	--	--	
3	4.3	13.7	4.0	15.3	unsuccessful	--	--	--	
4	4.2	12.0	5.8	15.5	unsuccessful	--	--	--	
5	5.2	13.8	4.7	15.8	unsuccessful	--	--	--	
6	6.5	11.7	5.7	11.8	successful	34.71	0	0	
8	6.5	13.0	5.3	13.2	unsuccessful	--	--	--	
9	5.2	11.5	4.5	11.7	unsuccessful	--	--	--	
10	4.5	13.3	4.8	13.8	unsuccessful	--	--	--	
11	5.8	10.7	4.0	13.8	unsuccessful	--	--	--	
12	5.2	10.7	4.0	10.8	unsuccessful	--	--	--	
13	5.0	7.0	dead	--	successful	6.09	1.02	0.084	
15	1/	8.5	1/	5.0	successful	2.84	0	0	
246 ^{2/}	15.5	13.5	1/	1/	successful	8.19	30.03	1.833	

1/Not measured.

2/All trees from Fox Prairie plot except 246 which was from the Twin Buttes plot and was measured on July 23, 1974.

CONCLUSIONS

The most conclusive result of the present study is that defoliation reduced afternoon moisture stress in grand firs during the year that defoliation occurred, and in the area of the tree subject to defoliation. This result is hardly surprising because defoliation reduces the transpirational surface area and hence water loss from the crown. Conservation of water during the peak diurnal evapotranspiration period reduces moisture stress in the tree at this time.

Although the effects of defoliation were not statistically significant in the 2 years following foliage removal, there were some interesting trends. For example, defoliation appeared to play an important role in determining early morning PMS, being included in step three in the multiple regression analysis, and improving the coefficient of multiple determination by 12.8 and 4.5 percent in the 2 years, respectively (table 3). Above average precipitation in the winters and summers following defoliation³ may have prevented a significant increase in early morning PMS. Although the hypothesis, that defoliation causes rootlet mortality (Redmond 1959) which results in moisture stress in the years following defoliation, could not definitely be established, the above observations suggest that there was a tendency toward increased PMS which may become pronounced under drought conditions.

An interesting interaction was discovered between PMS, needle length, and percent defoliation. Trees under high moisture stress had shorter needles, suggesting that needle length may be adapted to moisture conditions in the tree. In addition, needle length was inversely related to percent defoliation. The product of these two effects should be a strong direct effect of defoliation on PMS. That this was not observed indicates that the tree compensates for the effect of defoliation, perhaps by producing shorter needles so as to minimize evapotranspiration. A similar reduction in crown area in white fir infected with *Fomes annosus* root decay probably accounts for the finding that the trees showed no increased early morning PMS until more than 95 percent of the roots were decayed (Ferrell and Smith 1976).

The suspected relationship between defoliation, high PMS in the following years, and attack by the fir engraver beetle could not be demonstrated because PMS was not significantly increased by the effects of defoliation. Also, trees which were attacked and killed by the bark beetle were not noticeably higher in PMS than those that survived. The mechanism through which defoliated trees become susceptible to fir engraver attack has yet to be determined; however, we suspect that carbohydrate or oxygen deficits may be involved.

³ Climatological data for 1974, 1975 from U.S. Environmental Data Service, Meacham, Oreg.

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